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GEOGRAPHIC VARIATION IN THE COMMON TODY-FLYCATCHER (*TODIROSTRUM CINEREUM*), WITH SPECIAL REFERENCE TO MIDDLE AMERICA

*Kenneth C. Parkes**

This paper is dedicated to Dr. Alexander Wetmore, on the occasion of his ninetieth birthday, 18 June 1976.

Since the description of *Todirostrum cinereum finitimum* by Bangs in 1904, this name has been used universally for the Common Tody-Flycatchers of the Middle American portion of the species' range, from southern México through Panamá. A few authors have commented on the variability of specimens from within this range. Ridgway (1907:365) stated: "After very careful examination and comparison of a series of 108 adults of this species, I am not able to confirm all the characters of this form [*finitimum*] as given by Mr. Bangs, especially the alleged differences in intensity of the yellow on the underparts, which to me seems, if any different, brighter in South American than in Mexican and Central American skins, instead of the reverse. The difference in coloration of the upper parts is also by no means constant, but there seems to be an average difference sufficient to separate the two series." Most recently, Wetmore (1972:522) wrote: "The subspecies *finitimum* in its typical form, in México and northern Central America, differs in being more greenish above, as compared to the grayer nominate *cinereum* of northern South America. The population of Panamá is slightly intermediate, but on the whole is nearer *finitimum* in somewhat greenish dorsal hue, though many are faintly paler than typical individuals from México. The long series examined shows too much variation to warrant another name."

Early authors, such as Ridgway, were handicapped in their evaluation of geographic and individual variation in color in this species because they were not aware of its sexual dimorphism: Ridgway (1907:364) stated simply "sexes alike." Wetmore (1972:520) gave a detailed description of the plumage colors of males, and then correctly stated "Adult female similar, but usually with loral and frontal area with more tipping of yellowish white (this found also in some

*Chief Curator, Life Sciences
Carnegie Museum of Natural History

Library of Congress
Card No. 76-14378

males), and dorsal surface often paler, more grayish green." He went on to describe the perishable "soft part" colors of one male and one female specimen. The bills of these two he described as follows: male, "extreme tip of maxilla, lower half of mandibular rami, a line on the gonys, and tip of mandible ivory-white; rest of bill black." Female, "maxilla black; mandible dull white with a faint grayish tinge." This sexual dimorphism in mandible color is so consistent in adults of most races of this species that I have had no hesitation in considering the few pale-billed "♂" or black-billed "♀" specimens as having been missexed. The material of *T. c. peruanum* Zimmer in the American Museum of Natural History suggests that, in this race alone, both sexes have black mandibles. Dickey and van Rossem (1938:389) called attention to sexual dimorphism in bill color in *T. c. finitimum,* but believed that it also held true in juveniles; specimens I have examined suggest that bill color is *not* reliable for external sexing of young specimens. Dickey and van Rossem also overlooked the difference between the sexes in back color, correctly described by Wetmore, but instead stressed the greater posterior extension of the black crown color of males. This is a valid but somewhat variable character.

It is true that there is individual variation in dorsal color in this species, and color changes are produced with feather wear as well. However, when fresh specimens are examined in series, it becomes obvious that there is geographic variation within the Middle American range currently assigned to *finitimum*. Part of the difficulty previous authors have had in assessing this variation undoubtedly lies in the assumption that "Mexican" specimens can be considered topotypical and compared with specimens from elsewhere. As will be shown, the Common Tody-Flycatchers of México by no means represent a homogeneous population.

Both Ridgway (1907:364) and Wetmore (1972:522) mentioned the slightly larger size of South American as compared with Middle American specimens. Measurements *among* Middle American samples show only one definite geographically correlated trend, to be discussed later. Color of underparts, as already suggested by Ridgway, is virtually useless as a taxonomic character. I have relied entirely on the color of the upperparts (crown, dorsum, wing) in making my detailed comparisons.

In México this species is, in general, a bird of coastal lowlands. On the Caribbean side it extends northwest to the vicinity of the Río Papaloapan, Veracruz; if it goes beyond this area, I have not seen the records, nor are any known to Allan R. Phillips (*in litt.*). I have already commented (Parkes, 1970:93) on the status of the species on the Yucatán Peninsula. At that time I knew of no authentic record from the state of Yucatán earlier than a sight record at Sisal by Dale A. Zimmerman, 9 May 1956. I overlooked a specimen in the National Museum of Natural History (USNM 213146) taken by Gaumer at Progreso in October 1884 (Gaumer's specimens *with full data* are generally

reliable; see comments in Parkes, 1970) and another from Progreso in the Museum of Zoology, University of Michigan, collected by Van Tyne and Trautman on 14 May 1938. Paynter (1955:201) also overlooked these Yucatán specimens, listing this species as known from the Peninsula only from one locality in Campeche and four in Quintana Roo. It is possible that the status of this tody-flycatcher has changed in coastal Yucatán, as it has been seen and collected so frequently during the past two decades that it is difficult to understand how earlier observers could have missed it.

On the Pacific side of México, *Todirostrum cinereum* appears to be confined to the narrow coastal strip of the state of Chiapas. Beyond México it was stated by Land (1970:230) to be common in the Pacific lowlands of Guatemala and fairly common in the Caribbean lowlands and Petén district of that country, common in cleared and open areas of British Honduras (Russell, 1964:126), common below 1500 feet in El Salvador (Dickey and van Rossem, 1938:388), common in the Caribbean lowlands and uncommon in the interior and in the Pacific lowlands of Honduras (Monroe, 1968:273), and common in nonforested areas throughout most of Costa Rica (but not above the subtropical belt) (Slud, 1964:264). In Panamá, Wetmore (1972:520-521) considered this species "common in open, bushy areas in the Tropical Zone" and also "not abundant . . . [but] widely distributed so that they are seen regularly, mostly in pairs." Wetmore's distributional account suggests a hiatus in the range of this species in eastern Panamá, but this may be an artifact of collecting–the open or second-growth habitat preferred by this species is probably sparse in the relatively little-known eastern part of the country. Distribution within Panamá will be further discussed later in the present paper.

Although, as indicated earlier, this species is indeed rather individually variable in color, sex for sex, and severe wear obscures differences in back color, nevertheless the abundant material in adequate plumage condition available by pooling museum series has permitted the discrimination of three subspecies dividing up the range presently assigned to *T. c. finitimum.* Color differences are better marked among females, so specimens of this sex have been chosen as holotypes of the two new races.

Todirostrum cinereum viridiidorsale **new subspecies**

Holotype DMNH 54678, ♀ just completing 1st prebasic molt, collected 3–4 miles ENE of Tlacotalpan, Veracruz, México, on 24 September 1961, by Robert W. Dickerman; prepared by Allan R. Phillips (orig. no. ARP 5981).

DIAGNOSIS: Differs from *T. c. finitimum* Bangs in the much brighter, greener, less gray color of the back in both sexes but especially in females; crown in females more uniformly black, with little or no contrasting gray nuchal area and individual feathers of crown more uniform (in that they lack contrasting gray edgings in fresh condition); dorsal color nearest the geographically distant *T. c.*

coloreum Ridgway of Matto Grosso, Brazil, and adjacent eastern Bolivia, but crown blacker and size much smaller than in that subspecies. There is no significant difference in wing or bill length between *viridisdorsale* and *finitimum.*

RANGE: Known only from the drainage of the Río Papaloapan, in south-central Veracruz and adjacent northernmost Oaxaca, México.

ETYMOLOGY: From Latin *viridis,* "green," and *dorsalis,* "of the back," with reference to the most distinctive character of this race.

SPECIMENS EXAMINED: **México**, *Veracruz*–vicinity of Tlacotalpan 8, Tres Zapotes 2, Carlos A. Carrillo (formerly San Cristobal) 1; *Oaxaca*–Loma Bonita 2 (the record from San Miguel Soyaltepec listed by Miller et al. [1957:98] undoubtedly belongs here).

Todirostrum cinereum finitimum **Bangs**

Proc. Biol. Soc. Wash., **17**:114, 1904 (San Juan Bautista = Villahermosa, Tabasco, México).

DIAGNOSIS: Dorsal color of females variable, greenish gray to grayish green, but never the bright green of *viridisdorsale;* dorsal color of males darker and grayer, often with very little green element visible, so that the dorsal color appears almost continuous with the dark gray of the nape (the dorsal color of *finitimum* is actually nearest that of *T. c. cinereum* [Linnaeus] of South America, but the latter is usually darker, grayer, and more uniformly colored, with less tendency toward a brightening and greening in the rump area); shiny black area of anterior part of crown more restricted. The black feathers of the anterior half of the crown of females are edged with gray, especially posteriorly, so that this part of the crown appears in good light to be streaked. This pale edge is less resistant to wear than is the black center of the feather, so that worn females still have a streaked-crowned appearance, as the formerly pale-edged feathers wear narrower than the all-black crown feathers of *viridisdorsale.* This streaked-crowned appearance is visible in a few males, but in this sex the entire crown is usually black.

RANGE: From southern Veracruz through all of Central America, including the Yucatán Peninsula, to Costa Rica, on the Caribbean side, and north to Chiapas on the Pacific side; confined chiefly to coastal lowlands at the northern end of the range, but more widely distributed farther south. Intergrades in Costa Rica with the Panamanian race described later in this paper.

REMARKS: The restricted range of *Todirostrum cinereum viridisdorsale* is to some extent cut off from that of *T. c. finitimum* by the highlands of the Sierra de Tuxtla, Veracruz, although it is quite possible that the ranges of the two subspecies meet somewhere south or southwest (= inland) of these coastal mountains (see map in Wetmore, 1943:217). I have seen only one specimen from the eastern lowlands of Veracruz, between the Sierra de Tuxtla and the Tabasco border. This specimen (UMMZ 100231) is a female from Minatitlán and is clearly referable to *finitimum.* The population of the Pacific coastal lowlands of

Chiapas is completely isolated by highlands from other Mexican populations of the species but is inseparable from *finitimum* in color. This isolation does manifest itself in larger size, however—the only definitely geographically correlated size variation found in Middle American populations. Both in wing (flat) and bill (from forehead) length, the Chiapas birds are significantly larger, although not at a subspecific level of separability. For five Chiapas ♂♂, wing $\bar{x}$ = 44.3 mm., S.D. 0.67. For eight *finitimum* ♂♂ from Mexico, British Honduras, and Honduras, wing $\bar{x}$ = 43.4 mm., S.D. 0.51. For these two samples, Student's t = 2.756, $P < .02$. Bill differences are somewhat greater than wing: five Chiapas ♂♂, bill $\bar{x}$ = 16:0 mm., S.D. 0.42. For eight *finitimum,* bill $\bar{x}$ = 15.3 mm., S.D. 0.57. For these two bill samples, t = 3.215, $P < .01$.

This Chiapas population is geographically continuous with that of Pacific Guatemala. According to Land's map (1970:230), the central highlands create a divided range for this species in Guatemala as in Chiapas. I have examined only two specimens from Pacific Guatemala (AMNH 399195, 399196); these match the largest Chiapas specimens in wing length, but have even longer bills: ♂ 18 mm. (longest Chiapas = 16 mm.), ♀ 17.5 mm. (longest Chiapas = 15.9 mm.). For the present, these Pacific birds are best kept in *finitimum.*

SPECIMENS EXAMINED: **México**, *Veracruz*—Minatitlán 1; *Tabasco*—Frontera 3, San Juan Bautista (= Villahermosa) 2 (paratypes), La Venta 2, Teapa 1, Montecristo 1 (plus additional Tabasco specimens, not individually listed, seen at Louisiana State University); *Yucatán*—Progreso 2, Chelem 2, Chicxulub Puerto 1, unspecified 1; *Quintana Roo*—Vigia Chico 4; *Chiapas*—Pijijiapan 5, Escuintla 3, Huehuetan 1, 44 km. N Mapastepec 1, Palenque 1. **Guatemala**, *Petén*—various localities 6; *Escuintla*—Pantaleón 1, San José 1. **British Honduras** (= Belize)—All Pines 4, Freetown 3, Toledo District 1. **Honduras**—La Ceiba 4, Río Segovia 3, Coyoles 2, San Esteban 2, Lake Yojoa 1, Trujillo 1. **Nicaragua**—Greytown 3, Sucuya 1, Los Sabalos 1. **Costa Rica**—see under next subspecies.

Todirostrum cinereum wetmorei new subspecies

Holotype USNM 460905, adult ♀, collected at San Félix, Chiriqui, Panamá, on 13 February 1956, by Alexander Wetmore (orig. no. 20608).

DIAGNOSIS: Dorsal color nearer to *T. c. viridídorsale* than to the adjacent *T. c. finitimum,* but distinctly darker, less yellowish green, sex for sex; greener than the dark grayish *finitimum;* crown streaking as in *finitimum.*

RANGE: Panamá and much of Costa Rica. Most specimens from central and eastern Costa Rica are nearest to *wetmorei,* whereas those of northwestern Costa Rica are nearer *finitimum.* Interestingly, the transition in females is much more abrupt than in males, with almost all Costa Rican females except those from Guanacaste being much closer to *wetmorei,* whereas the Costa Rican males as a group are variable intermediates. I have therefore not tried to segregate Costa

Rican specimens by subspecies names and intergrades, but list them all later under the SPECIMENS EXAMINED heading for *wetmorei.*

ETYMOLOGY: Named for Dr. Alexander Wetmore of the Smithsonian Institution, the greatest American ornithologist of the twentieth century, authority on the birds of Panamá, and a friend and mentor to hundreds of younger colleagues.

REMARKS: The series of *wetmorei,* like all other series of this species, is somewhat individually variable in color, with females being more consistent than males. There is no indication of any cline from western to eastern Panamá. The two Darién specimens examined cannot be separated from the rest of the Panamanian series and do not approach *cinereum* of adjacent South America. Furthermore, birds from the Río Atrato, in Colombia adjacent to Panamá, do not approach *wetmorei* (contrary to the statement of Chapman [1917:437-438]); in fact, one specimen (CM 64401) from Quibdó on the upper Atrato is virtually as blackish above as the extremes among all South American *T. c. cinereum* examined.

SPECIMENS EXAMINED: A long series of Panamá specimens in USNM were looked over; those listed were used for detailed comparisons as being in good plumage, or as to fill in locality gaps. **Panamá**, *Bocas Del Toro*–Almirante 6, Cocoplum 3; *Chiriquí*–El Volcan 5, Boquerón 3, San Félix 2, Alanje 1, Boquete 1, Cerro Flores 1, Puerto Armuelles 1, Sereno 1; *Veraguas*–Isla Coiba 2, Chitrá 1, Isla Cebaco 1, Isla Gobernadora 1, 15 miles SE Santiago 1, Soná 1; *Herrera*–El Rincón 1; *Los Santos*–Los Santos 1; *Coclé*–Aguadulce 2, El Potrero 1; *Colón*–Chilar 2; *Panamá*–Chico 3, Savanna near Panamá 2, Candelaria 1, La Chorrera 1, Pacora 1; *Canal Zone*–Gatún 2, Fort Clayton 1, Juan Mina 1; *San Blas*–Mandinga 1; *Darién*–Boca de Cupe 1, Cana 1. **Costa Rica**, *Limón*–Guápiles 11, Guácimo 2, Río Reventazón 2, El Hogar 1, Jiménez 1; *Guanacaste*–Guayabo 3, Miravalles 2, Zapotal 1; *Puntarenas*–Buenos Aires 2, Bonilla 1, Orotina 1, Pigres 1; *San José*–Carrillo 2, San José 1; *Cartago*–Aquiares 2, Juan Viñas 2, Pacuare 1.

NOTES ON SOUTH AMERICAN POPULATIONS

A not uncommon variation in this species is the presence of one or more white feathers in the black crown area. This variation appears to be independent of age or sex and may appear anywhere in the range of the species–I have seen it in *viridiidorsale* from Veracruz and in *coloreum* from Bolivia, as well as from various intermediate localities. In the series of the species now before me, this variation occurs most frequently in specimens from north-central Venezuela (states of Carabobo, Aragua, Miranda, and the Distrito Federal): of 37 specimens from this region, 13, or 35.1 per cent, exhibit one or more crown spots, whereas in the total series of 142 from the rest of the range of the species, only 15, or 10.6 per cent, have crown spots. The high frequency of white crown spots in this

northern Venezuela sample suggests affinity with the highly distinctive form *viridanum* of the westernmost coastal areas of Venezuela, in the states of Zulia and Falcón. This form, described by Hellmayr (1927:301) as a full species, is differentiated from the adjacent *T. c. cinereum* by several characters, one of which is "some of the feathers on the anterior crown spotted with creamy white." Rodolphe Meyer deSchauensee (1966:363) and other recent authors have placed *viridanum* as a subspecies of *cinereum.*

The nominate race, according to current concepts, occupies tropical and lower subtropical areas of suitable habitat in Colombia (except southernmost), Venezuela (other than in the small range of *T. c. viridanum*), the Guianas, and northern Brazil. There is some geographically correlated variation within this area, but I have not yet been able to define any pattern that would make geographic sense. At the north end of Lake Maracaibo, Venezuela, and extending along the coast of the state of Falcón, lies the range of the pale, strikingly marked race *viridanum* Hellmayr. Nearby, between the southern end of Lake Maracaibo and the Mérida mountains, there is apparently a center of differentiation in the exact opposite extreme of color. In a small series in Carnegie Museum of Natural History (CM) from the western foothills of the Mérida mountains, in west-central Estado Mérida, both sexes are much sootier above than typical *T. c. cinereum* from the Guianas, with *no* greenish tones whatsoever on the dorsum except on the upper tail-coverts. In addition, the shiny black (anterior) portion of the crown extends farther caudad and is more glossy than in most other *cinereum.* The tiny feathers between the forehead and the nostril that are yellow in most females and some males of this species are, in the Mérida birds, black with little or no yellow.

I have refrained from naming this Mérida population for two reasons: first, more specimens from adjacent areas must be examined to see how far this tendency to blackness extends; and second, the nearest approach to the characters of the Mérida birds among the South American specimens I have examined is found in two series from Chocó, in northwesternmost Colombia (CM, ANSP). This area is separated from Mérida by much of the Colombian range of the species, from which the available specimens are indistinguishable from Guianan *cinereum.* It is obvious that a reexamination of variation in *Todirostrum cinereum* in northern South America is warranted.

SUMMARY

"Individual variation" in *Todirostrum cinereum finitimum* Bangs of Middle America noted by other authors is attributable in part to overlooked sexual dimorphism and in part to the assumption that all Mexican specimens could be considered topotypical of *finitimum.* The population of the Río Papaloapan drainage of Veracruz and adjacent northern Oaxaca, at the northern extreme of the species' range, is distinct and is described as *T. c. virididdorsale* ssp. nov. The

population of Panamá and most of adjacent Costa Rica is also separable and is named *T. c. wetmorei* ssp. nov. Trends in geographically correlated variation within *T. c. cinereum* (Linnaeus) of northern South America are outlined.

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